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Original article

Bouleiceras (Hildoceratidae, Ammonitina) from the lower Toarcian (Jurassic) of the Iberian Range (Spain): Taxonomy, stratigraphic distribution and insights on its dispersal☆

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ABSTRACT

Bouleiceras is a very rare genus among the rich assemblages of ammonoids from the lower Toarcian of the Iberian Range. So far, only two dozen specimens have been recorded in numerous field campaigns carried out since 1965 by different authors. The interest of this taxon lies in its peculiar paleogeographical distribution in comparison with most other ammonoids of the same age. A review of these specimens is carried out, including those obtained in previous works and others recently collected in selected localities. Based mainly on the differences in the shape of the ventral section and the suture line, seven species have been identified; two of which are new: *Bouleiceras ibericum* nov. sp. and *Bouleiceras? betetensis* nov. sp. All the reviewed specimens are recorded in the Semicelatum Subzone of the Tenuicostatum Zone and the Elegantulum Subzone of the Serpentinum Zone from the Central Sector and the Levantine Sector of the Iberian Range. The global distribution of the genus is summarized from the known data, and its possible dispersal routes are analyzed, as well as the factors that could have conditioned them.

Introduction

The genus *Bouleiceras* Thévenin, 1906 is an exotic member of some ammonoid assemblages of the Lower Jurassic of Western Tethys, whose presence does not seem to fit well with the provincialism established in the region during most of the Mesozoic. Until the 1950s, it was only known from Madagascar, where the type species *Bouleiceras nitescens* Thévenin, 1906, was described by Thévenin (1906, 1908), Collignon (1958), and Blaison (1968). Afterwards, this and other species assigned to *Bouleiceras* have been recognized in different basins of Northeast and Northwest Africa, Arabia, the Indian subcontinent, the Iberian Peninsula, and South America. In Arabia, *Bouleiceras* was recorded in several localities by Steinecke and Bramkamp (1952) and described by Arkell (1952) who defined several new species, as well as by Enay and Mangold (1994). All these records come from the Lower Marrat Fm., where they appear together with *Protogrammoceras madagascariense* (Thévenin) and *Calyptoria* sp., the same association found in Madagascar (Basse and Karpoff, 1957). In Northeast Africa it has been cited in Kenya (Ayers, 1952; Arkell, 1956) and in the Uanei Fm. in Somalia (Chiocchini et al., 2002). In Pakistan, *B. nitescens* and another species *B. chakdallaense* Fatmi, 1972, have been recorded (Davies and Gardezi, 1965; Fatmi, 1972; Fatmi and Hölder, 1975). Outside the Indo-Madagascan Area, *Bouleiceras* has been cited in the Western Tethys area in Portugal (Mouterde, 1953; Dubar and Mouterde, 1953; Mouterde and Rocha, 1981), in the Iberian Range in Spain (Geyer, 1965, 1971; Behmel and Geyer, 1966; Bizon et al., 1966; Dubar et al., 1970; Mouterde, 1970, 1971; Marin and Toulouse, 1972; Goy, 1974, 1975; Herrero-Organero, 1986; Goy et al., 1988; Herrero Matesanz, 1995; Goy and Martínez, 1996; Martínez, 2017a) and in the Pre-Rif of Morocco (Faugères, 1975). In addition, the genus has been recorded in Chile (Hillebrandt, 1973, 1984, 1987; Hillebrandt and Schmidt-Effing, 1981). The stratigraphic position of all these records has been considered in the interval between the upper Pliensbachian Spinatum Zone and the lower Toarcian Serpentinum Zone.

The aim of the present paper is to review the fossils attributed to *Bouleiceras* recorded in the Iberian Basin. For this purpose, its taxonomy has been updated and its stratigraphic distribution has been accurately established. The global stratigraphic distribution

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of the species of this genus is also discussed from the available data, as well as the possible factors that triggered its geographical dispersion.

Studied material

The Bouleiceratinae represent less than 3% of the Hildoceratidae and 1% of the total of the ammonoids recorded in the lower Toarcian of the Iberian Range. The studied specimens belonging to *Bouleiceras* have been collected during the realization of regional works and doctoral theses, between 1965 and 1996, by different authors (Comas-Rengifo, Fernández-Lopez, Goy, Herrero Matesanz, Herrero-Organero, Suárez Vega, and Meléndez) in the central sector of the Iberian Range (Fig. 1). Most of the specimens obtained in these works are currently deposited in the Paleontological collections of the Complutense University of Madrid, including the specimens identified as *B.* cf. *tumidum* Arkell, 1952, and *B. nitescens* Thévenin, collected by Mouterde (1971: p. 349) in Obón (Teruel). Specimens collected by Herrero-Organero and Suárez-Vega in Moneva (Zaragoza) and deposited in the Jurassic Museum of Asturias (MUJA) have been also reviewed, and the specimens figured by Geyer (1965: pp. 27, 28, pl. 5, figs. 1–3) as *B. arabicum* Arkell, 1952, *B. marraticum* Arkell, 1952, and *B.* cf. *elegans* Arkell, 1952 from Albarracín (Teruel), as well as *B. nitescens* figured by Bizon et al. (1966: p. 902, pl. 27a, fig. 7a-c) from Tavernes de la Valldigna (Valencia), in the Levantine Sector of the Iberian Range, have also been considered in the revision. Besides this, new specimens have been collected during the last years in the sections of Ariño (Teruel), Moneva (Teruel), Turmiel (Guadalajara), and Valsalobre de Beteta (Cuenca). Some isolated or "ex situ" specimens have also been collected in Albarracín (Teruel), Entrambasaguas (Teruel), Ribarredonda (Guadalajara), Ablanquejo (Guadalajara), Calanda (Teruel), and Barahona (Soria).

Stratigraphic framework

All the specimens come from the Turmiel Fm. (Goy et al., 1976). This formation is composed by the alternation of marls and mudstone carbonates, which are organized into sets of deepening and shallowing-upwards sequences (Gómez and Goy, 2000). Sequentially, the sedimentation of this unit started with a generalized transgressive event during the early part of the Tenuicostatum Zone that reached its maximum deepening at the middle part of the Bifrons Zone. Nevertheless, the transgression is not represented by a continuous simple deepening episode, but by several pulses (Gómez and Goy, 2000, 2005). There are two cycles and the transgressive maximum of the first one is at the Elegantulum Subzone, resulting in the establishment of external platform environments facilitating the transport of ammonite shells by drift into most of the area of our studies.

Most of the *Bouleiceras* specimens recorded in the Iberian Range come from the interval between the Semicelatum Subzone of the Tenuicostatum Zone and the Elegantulum Subzone of the Serpentinum Zone. The biostratigraphic scheme used in this work follows Goy et al. (1988) and the standard chronostratigraphic reference scales for the Toarcian proposed by Elmi et al. (1997) and Page (2003). The succession of biohorizons (Figs. 2,3) corresponds to the regional data derived from Comas-Rengifo (1982) for the Pliensbachian and from Goy et al. (1988), Goy and Martínez, 1990Goy and Martínez (1990), Comas-Rengifo et al. (2010), as well as unpublished data, for the lower Toarcian. Figs. 2 and 3 show the precise stratigraphic position of the *Bouleiceras* species collected in the referenced sections.

Systematic paleontology (G. Martínez)

Order Ammonitida Fischer, 1882
Suborder Ammonitina Fischer, 1882
Superfamily Hildoceratoidea Hyatt, 1867
Family Hildoceratidae Hyatt, 1867
Subfamily Bouleiceratinae Arkell, 1950
Genus ***Bouleiceras*** Thévenin, 1906

Type species: *Bouleiceras nitescens* Thévenin, 1906. Lectotype in Thévenin (1908: pl. 2, fig. 6a, b), coming from Bekoratsaky, Maevatanana, Madagascar.

Other included species: *B. tumidum* Arkell, 1952; *B. arabicum* Arkell, 1952; *B. marraticum* Arkell, 1952; *B. elegans* Arkell, 1952; *B. rectum* Arkell, 1952; *B. chakdallaense* Fatmi, 1972; *B. chilense* Hillebrandt 1973; *B. ibericum* nov. sp.; *Bouleiceras? betetensis* nov. sp.

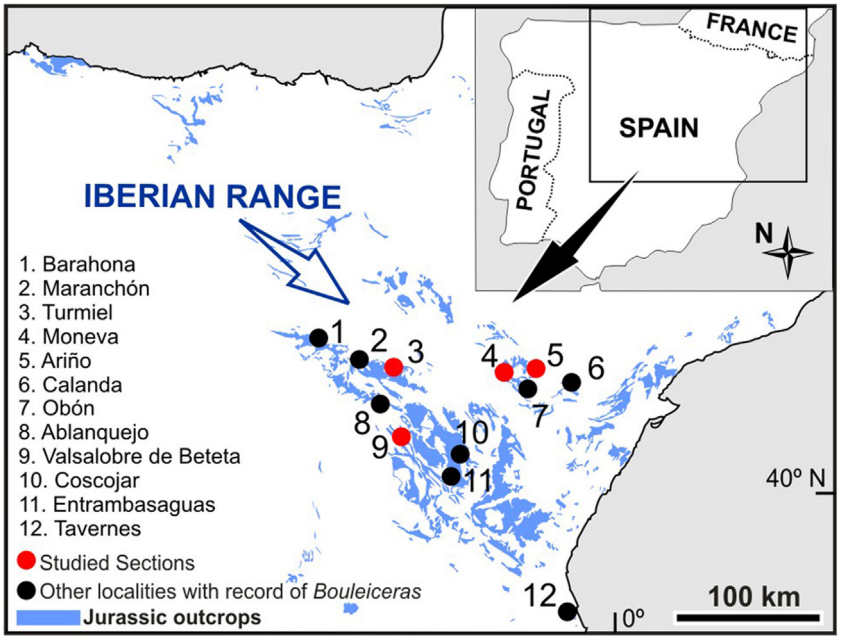

Fig. 1. Geographical location of the lower Toarcian sections mentioned in the text.

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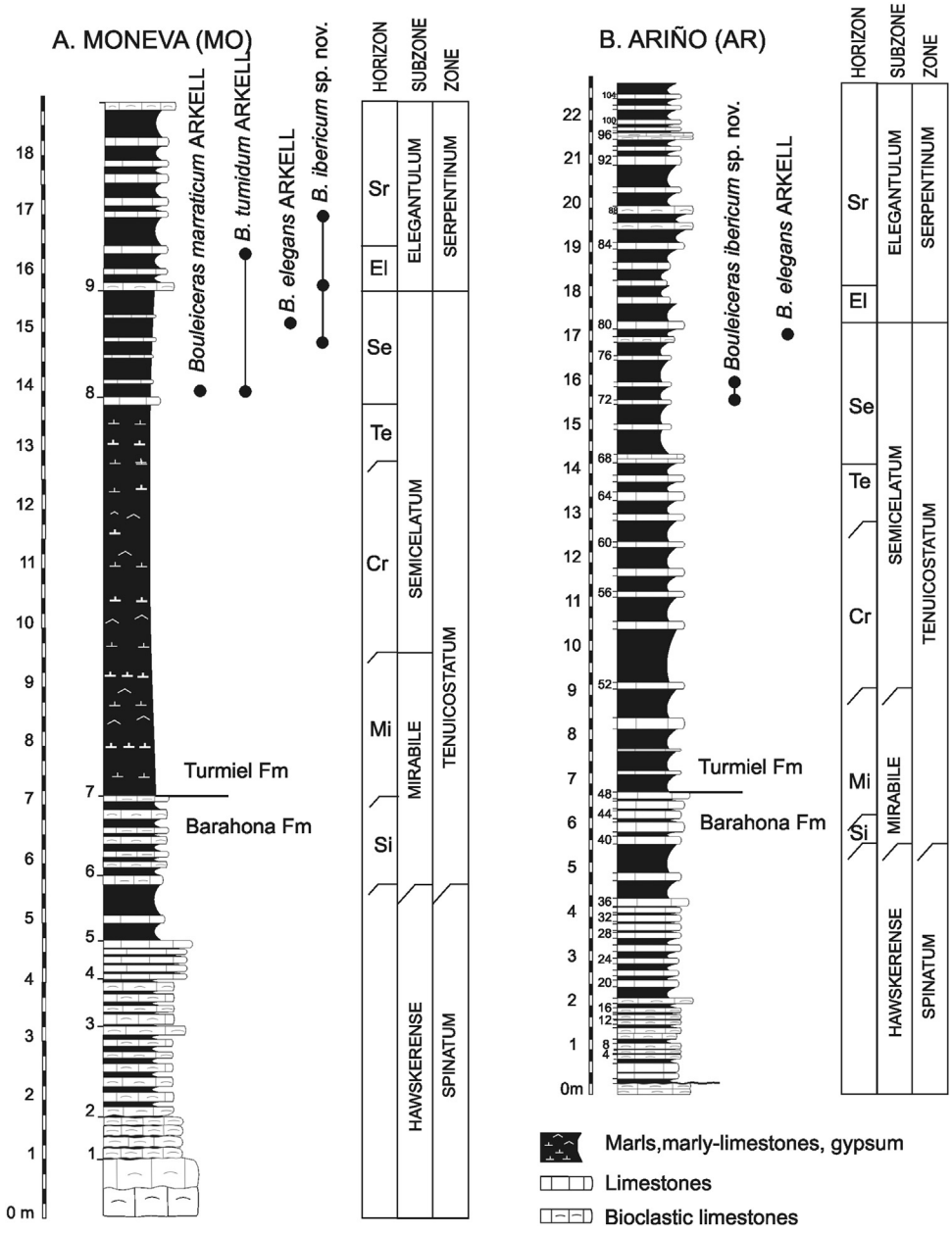

Fig. 2. A. Valsalobre de Beteta Section (VA), showing the beds that yield *Bouleiceras* species (modified after Goy, 1974). **B**. Turmiel Section (TU), showing the beds that yield *Bouleiceras* species (modified after Goy, 1974 and Comas-Rengifo et al., 2007). Si: Simplex; Mi: Mirabile; Cr: Crosbeyi; El: Elegantulum; St: Serpentinum. In both sections the boundary between the Barahona and Turmiel formations is indicated.

Remarks: According to the diagnosis given by Howarth (2013: p. 81), this genus is:"*evolute, coronate inner whorls, becoming more involute, planulate, and compressed on outer whorls; strong ventral keel throughout; innermost whorls are smooth, followed by a uni- or bituberculate stage, with or without ribs, then a stage with strongly rursiradiate, straight or sinuous ribs that bifurcate from umbilical tubercles, and finally a flat-sided smooth adult stage; sutures ceratitic, with wide entire saddles, and a deep digitate first lateral lobe*".

Bouleiceras nitescens Thévenin, 1906

Fig. 4(A-D)

1906. *Bouleicera nitescens* n. sp. - Thévenin, p. 171, figs. 1–3.

1908. *Bouleiceras nitescens* Thévenin - Thévenin, p. 13, pl.2, figs. 6 (lectotype), 7 and 11?

1910. *Bouleiceras nitescens* - Haug, p. 995, fig. 308.

1952. *Bouleiceras nitescens* Thévenin - Arkell, p. 261, pl. 15, figs. 5a, b; text- fig. 4.

1953. *Bouleiceras* cf. *nitescens* Thévenin - Mouterde, p. 7, pl. 1, fig. 1a, b.

1958. *Bouleiceras nitescens* Thévenin - Collignon, pl. 1, figs. 1–3.

1966. *Bouleiceras nitescens* Thévenin - Bizon et al., pl. 27a, fig. 7a-c.

1971. *Bouleiceras nitescens* Thévenin - Mouterde, p. 349.

1974. *Bouleiceras nitescens* Thévenin - Goy, p. 570, pl. 40, fig. 2 a-c.

1974. *Bouleiceras* cf. *nitescens* Thévenin - Comas-Rengifo, p.129, pl. 14, fig. 2a, b.

?1981. *Bouleiceras nitescens*? Thévenin - Mouterde and Rocha, p. 219, pl. 2, fig. 2a, 2b.

Material: Specimens Ab-11/1; Tu-10.2/3; 2Eb-10.28/1; Ob-14B/1. All specimens are incomplete phragmocones.

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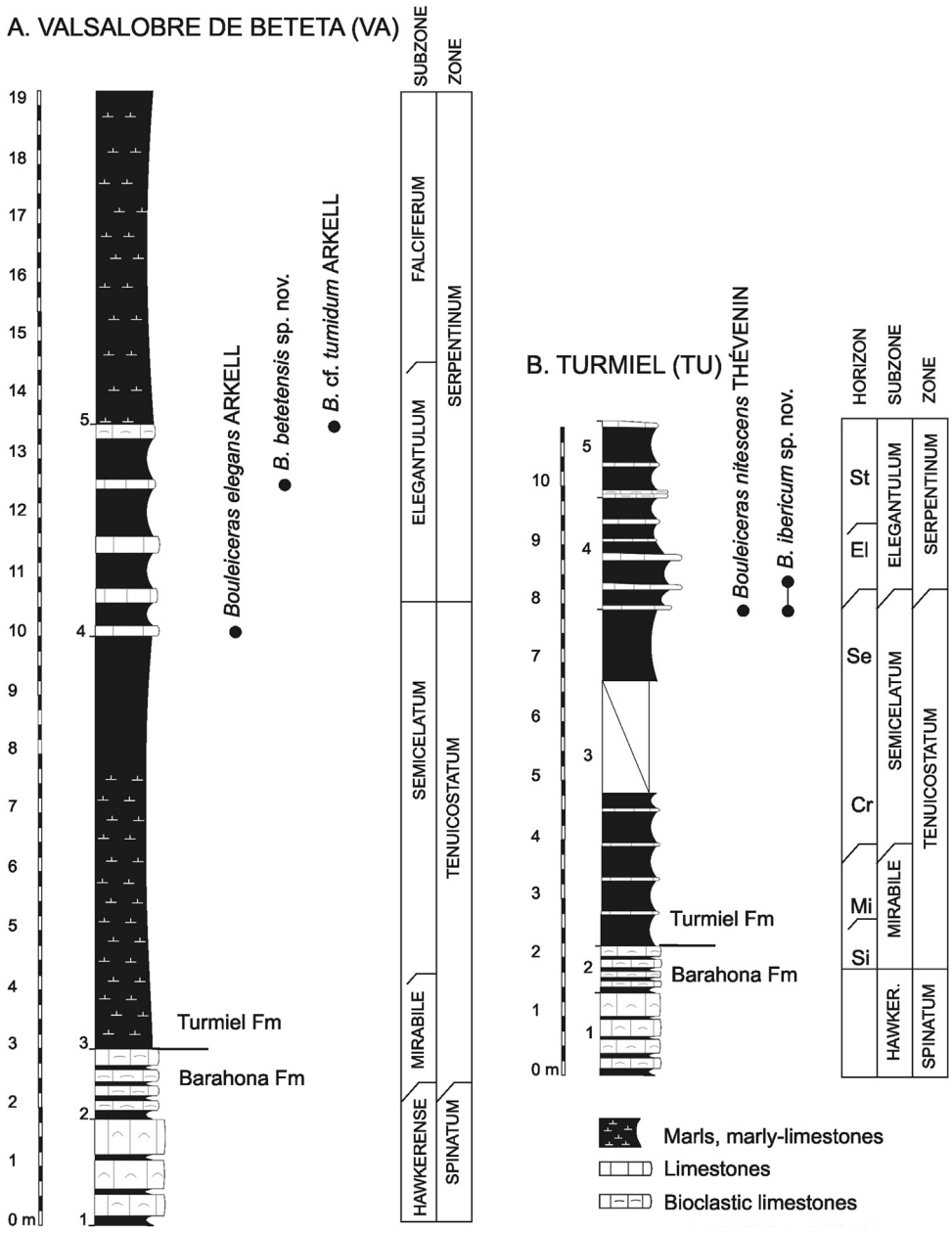

Fig. 3. A. Moneva Section (MO), showing the beds that yield *Bouleiceras* species **B**. Ariño Section (AR), showing the beds that yield *Bouleiceras* species (modified after Osete et al., 2007). Si: Simplex; Mi: Mirabile; Cr: Crosbeyi; El: Elegantulum; Sr: Serpentinum. In both sections the boundary between the Barahona and Turmiel formations is indicated.

Geographic and stratigraphic distribution: In the Iberian Range, this species has been recorded in the uppermost Semicelatum Subzone of the Tenuicostatum Zone in Turmiel, and in the Elegantulum Subzone of the Serpentinum Zone in Ablanquejo, Entrambasaguas and Obón. In Tavernes de la Valldigna, this species comes from Bizon et al.'s (1966) level 7 (6 m thick), associated with the brachiopods *Dispiriferina? oxyptera* (Buvignier, 1843), *Lobothyris arcta* (Dubar, 1931) and *Aulacothyris iberica* Dubar, 1931, species that in the Iberian Range only coexist in the Semicelatum Subzone of the Tenuicostatum Zone (García Joral and Goy, 2000; Baeza-Carratalá et al., 2016).

Measurements: see Table 1.

Description: Shell moderately evolute, whorl expansion rate (WER) between 1.81 and 1.96; subtrapezoidal compressed section, with maximum width close to the umbilicus and flat flanks. The ventral region presents a keel bordered by two shallow furrows. The umbilical area is relatively wide, with convex rounded edges. The ornamentation is marked in the first whorls, becoming more tenuous until disappearing in advanced stages; in internal whorls it is composed of rounded and spaced tubercles from which arise pairs of straight and retroverse ribs, somewhat finer than the intercostal spaces, protruding slightly before disappearing near the ventral region. Suture line with external saddle (ES) and external lobe (EL) narrow and deep; first lateral saddle (LS1) wide, smooth and divided by a narrow and short central lobe; LL1 somewhat smaller than LS1 with several sharp cuts in the posterior region and semi-parallel and smooth flanks; LS2 approximately equal in width than the LS1, smooth and rounded; LL2 narrow and sharp. In the umbilical edge, rounded saddles and acute lobes, all of small size, are observed as accessory elements.

Remarks: *B. nitescens* differs from *B. elegans* by its less evolute and compressed shell, more tuberculated in the phragmocone. It

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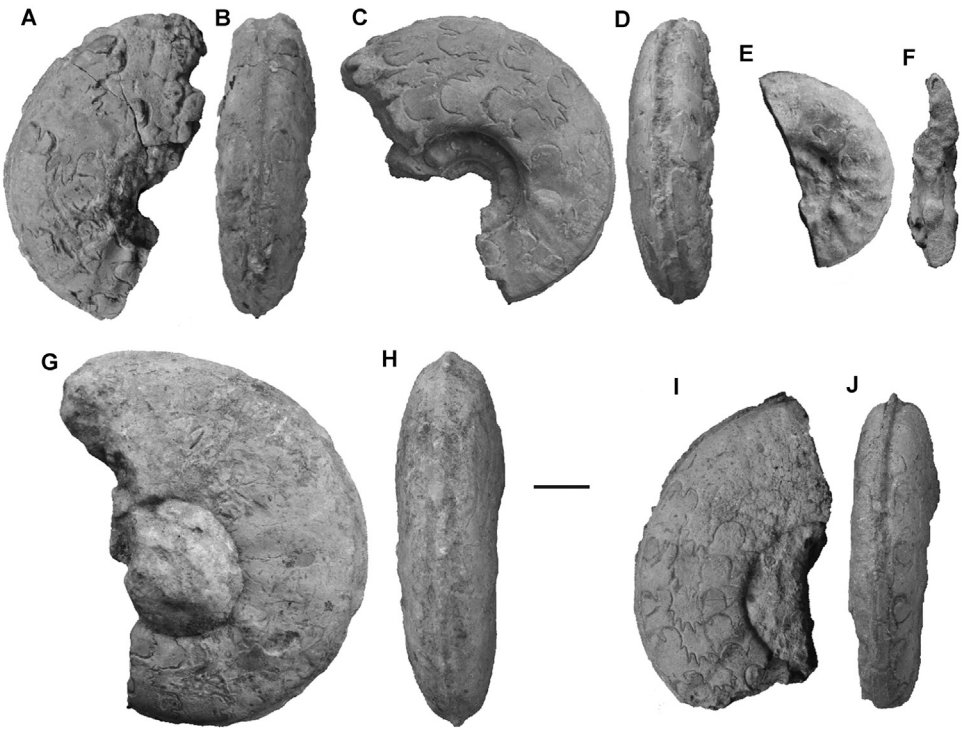

Fig. 4. A-D. *Bouleiceras nitescens* Thévenin, 1906. A, B: specimen Ab-11/1, Serpentimun Zone, Elegantulum Subzone, Ablanquejo, in lateral (A) and ventral (B) views; C, D: specimenTu-10.2/3, Tenuicostatum Zone, Semicelatum Subzone, Turmiel, in lateral (C) and ventral (D) views. **E-H**. *Bouleiceras elegans* Arkell, 1952. E, F: specimen Va4inf/1, Tenuicostatum Zone, Semicelatum Subzone, Valsalobre de Beteta, in lateral (E) and ventral (F) views; G, H: specimen Mo-8.2/1, Tenuicostatum Zone, Semicelatum Subzone, Moneva, in lateral (G) and ventral (H) views. **I, J**. *Bouleiceras arabicum* Arkell, 1952, specimen 1Ar-69/1, Tenuicostatum Zone, Semicelatum Subzone, Ariño, in lateral (I) and ventral (J) views. Scale bar: 1 cm.

Table 1
Measurements of the studied specimens of *Bouleiceras*. D: shell diameter; H: last whorl high; h: H/D; W: last whorl width; w: W/D; U: Umbilicus diameter; u: U/D; WER: whorl expansion rate: M= moderate; H= high (see Korn, 2010).

Specimen	D	H	h	W	w	U	u	WER
B. nitescens Thévenin, 1906								
Ab-11/1	59.8	24.7	0.41	19.8	0.33	21.2	0.35	1.81 M
Tu-10.2/3	56.3	22.5	0.4	17.1	0.3	20.4	0.36	-
	58.2	23	0.39	17.2	0.29	19.8	0.34	1.96 M
Ob-14B/1	67.3	26.9	0.4	19.3	0.29	24.2	0.36	1.89 M
B. elegans Arkell, 1952								
Mo-8.2/1	72.2	30.2	0.42	22.2	0.31	24.9	0.34	2.02 H
1Ar-76/1	120	47.3	0.39	30.7	0.23	49.4	0.4	2.14 H
B. marraticum Arkell, 1952								
Mo-7.20/2	22.4	8.9	0.39	8.2	0.36	9.7	0.43	1.96 M
Bouleiceras ibericum nov. sp.								
Tu-10.2/2	20.2	8.2	0.41	6.3	0.31	6.6	0.32	1.79 M

differs from *B. ibericum* nov. sp. in having a subtrapezoidal compressed section, tubercles in the inner whorls and the suture line more indented.

Bouleiceras elegans Arkell, 1952

Fig. 4(E-H)

1908. *Bouleiceras nitescens* - Thévenin, pl. 2, fig. 8 (holotype), 10.

1952. *Bouleiceras elegans* n. sp. - Arkell, p. 264, pl. 15, figs. 9,11a, b.

1958. *Bouleiceras elegans* Arkell - Collignon, pl. 1, figs. 5, 6.

?1958. *Bouleiceras rochi* nov. sp. - Collignon, pl. 3, fig. 22.

non 1965. *Bouleiceras* cf. *elegans* Arkell - Geyer, p. 28, pl. 5, fig. 2, text. fig. 1c.

1974. *Bouleiceras* cf. *elegans* Arkell - Goy, p. 569, pl. 40, fig. 3.

1986. *Bouleiceras* sp. - Herrero-Organero, p. 71, pl. 11, fig. 4.

1995. *Bouleiceras* sp. - Herrero Matesanz, p. 322.

Material: Specimens Mo-8.2/1, 1Ar-76/1 (incomplete phragmocones and part of the body chamber) and Cl-22/1, Va-4 in./1 (incomplete phragmocones).

Geographic and stratigraphic distribution: In the Iberian Range, this species has been recorded in the Semicelatum Subzone of the Tenuicostatum Zone of Valsalobre de Beteta, Moneva, Ariño and Calanda.

Measurements: see Table 1.

Description: Shell evolute, WER index between 2.02 and 2.14; subovoidal compressed section in the inner whorls, more flattened in the external one, with maximum width close to the umbilicus. The ventral region presents a high and thick keel bordered by two shallow furrows. Wide umbilical area, with rounded edges and flat vertical walls. The ornamentation is progressively more tenuous during the ontogenetic development, until disappearing in the body chamber. In the inner whorls it is composed of small and rounded tubercles close to the umbilical edge, from which single or double retroverse ribs arise, somewhat finer than the intercostal spaces, protruding slightly near the ventral region. In 1Ar76/1, two rows of tubercles joined by ribs are observed in the inner whorls. In the visible part of the suture line, EL is deep, narrow and acute, with the first lateral saddle (LS1) wide, smooth and divided by a narrow and short central lobe; the LL1 is somewhat smaller than LS1, trapezoidal with several sharp incisions; LS2 is rounded.

Remarks: *B. elegans* differs from *B. nitescens* by being more evolute and compressed, with weaker tubercles in the phragmocone.

Bouleiceras arabicum Arkell, 1952

Fig. 4(I, J)

1952. *Bouleiceras arabicum* n. sp. - Arkell, p. 262, pl. 15, figs. 6,8,13,14 (holotype).

?1958. *Bouleiceras arabicum* Arkell - Collignon, pl. 2, figs. 9,10,13,14, pl. 3, fig. 21.

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1965. *Bouleiceras arabicum* Arkell - Geyer, p. 27, pl. 5, fig. 1, text. fig. 1a.

?1975. *Bouleiceras* aff. *arabicum* Arkell - Faugères, p. 120, pl. 1, figs. 1a, b, 2a-c.

Material: Specimen 1Ar-69/1 (incomplete phragmocone and part of body chamber).

Geographic and stratigraphic distribution: The only specimen recorded in the Iberian Range comes from the Semicelatum Subzone of the Tenuicostatum Zone of Ariño.

Description: Shell evolute, the last whorl covering 1/3 of the previous one; compressed section with flat flanks, almost parallels but slightly convergent in the ventral area. Thin and high keel bordered by two flat bands. Wide umbilical area, with rounded edges and flat and strongly inclined walls. The ornamentation is composed by low retroverse ribs which arise in pairs from a slight thickening close to the umbilical border and disappear near the ventral region. In the visible part of the suture line, EL is thin and deep, LS1 does not show cuts and is divided by a short and acute lobe; LL1 is somewhat smaller than LS1, with semi parallel sides and several sharp cuts posteriorly; LS2 is smooth and rounded, smaller than LL1.

Remarks: The last whorls are similar in this species to those of *B. elegans*, although with the flanks flatter and almost parallel. According to Arkell (1952), the ventral area is tabulated in the inner whorls.

Bouleiceras tumidum Arkell, 1952

Fig. 5(A-F)

1908. *Bouleiceras nitescens* Thévenin - Thévenin, pl. 2, fig. 9 (holotype).

1952. *Bouleiceras tumidum* n. sp. - Arkell, p. 261.

?1965. *Bouleiceras* cf. *elegans* Arkell - Geyer, p. 28, pl. 5, fig. 2, text. fig. 1c.

1970. *Bouleiceras* cf. *tumidum* Arkell - Mouterde, p. 349.

Material: Specimens Mo-7.20/1, Mo-5.1-2/4, Ob-14/1, Va-5.1-2/1 (incomplete phragmocones).

Geographic and stratigraphic distribution: The collected specimens come from the Semicelatum Subzone of the Tenuicostatum Zone and the Elegantulum Subzone of the Serpentinum Zone of Moneva. The specimen identified by Mouterde (1970, 1971) comes from the Elegantulum Subzone of Obón.

Description: Shells slightly evolute, the last exposed whorl covering half of the previous one; sub-trapezoidal to sub-rectangular compressed whorl-section, with gently convex flanks and maximum width in the umbilical edge. The ventral area presents a keel bordered by two shallow and narrow grooves disappearing in the outermost whorls, making the keel thicker. Umbilicus wide, with rounded edges and convex walls. The ornamentation is composed by thick and low retroverse ribs, slightly wider than the intercostal spaces, arising from a slight thickening in the umbilical edge and disappearing before reaching the ventral region. This ornamentation is not present in the more adult specimen. In the visible part of the suture line, EL is deep, LS1 wide, without incisions, and divided by a short lobe not centered; LL1 is somewhat smaller than LS1 and slightly wider in its posterior part, with semi-parallel sides and several sharp incisions posteriorly; LS2 smooth and rounded, wider than LL1; LL2 is similar to LS2 but half its size and with two acute incisions in the posterior part.

Remarks: *B. tumidum* is more involute and present a more inflated section than *B. nitescens*. In the holotype, the tubercles in the inner whorls are stronger. The specimen labeled Va-5.1-2/1 (Fig. 5(E, F)) has been included with doubts in this species, because the suture line presents numerous small and rounded incisions in the saddles. It comes from the uppermost levels of the species distribution (Strangewaysi Horizon).

Bouleiceras marraticum Arkell, 1952

Fig. 5(G, H)

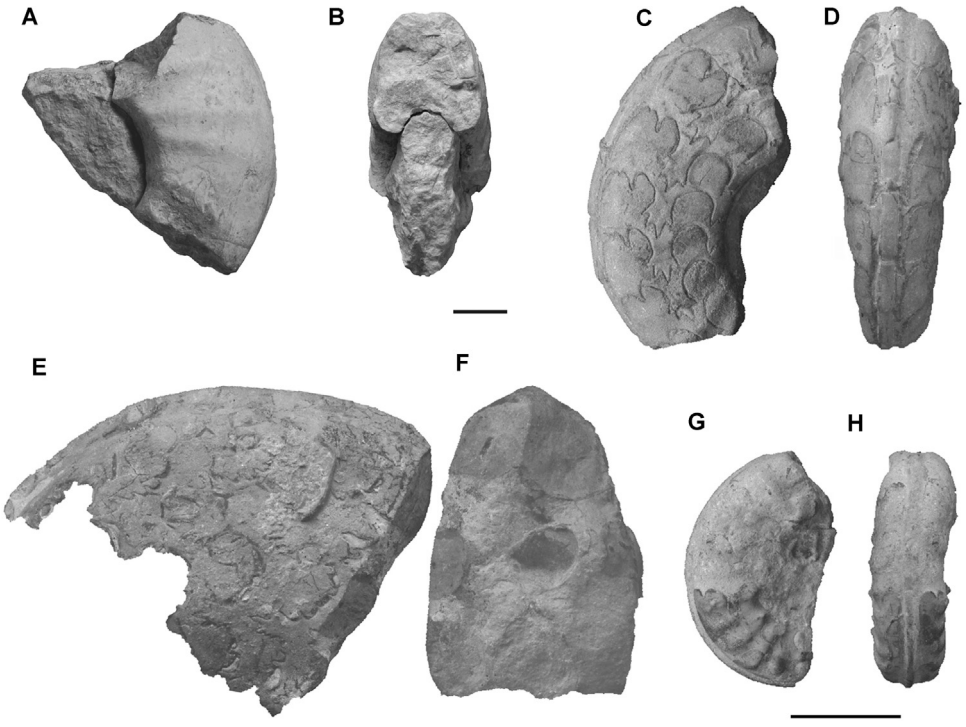

Fig. 5. A-F. *Bouleiceras tumidum* Arkell, 1952. A, B: specimen Ob-14/1, from the Serpentinum Zone, Elegantulum Subzone, Obón, in lateral (A) and ventral (B) views; C, D: specimen Mo-7.20/1, Tenuicostatum Zone, Semicelatum Subzone, Moneva, in lateral (C) and ventral (D) views; E, F: specimen Va-5.1-2/1, Serpentinum Zone, Elegantulum Subzone, Valsalobre de Beteta, in lateral (E) and ventral (F) views. **G, H**. *Bouleiceras marraticum* Arkell, 1952, specimen Mo-7.20/2, Tenuicostatum Zone, Semicelatum Subzone, Moneva, in lateral (G) and ventral (H) views. Scale bars: 1 cm.

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?1908. *Bouleiceras nitescens* Thévenin - p. 117, pl. 2, fig. 13.
1952. *Bouleiceras marraticum* n. sp. - Arkell, p. 263, pl. 15, fig. 10a-c (holotype).
1958. *Bouleicerras marraticum* Arkell - Collignon, pl. 2, fig. 12.
1965. *Bouleiceras marraticum* Arkell - Geyer, p. 58, pl. 5, fig. 3, text. fig. 1b,1d.

Material: Specimen Mo-7.20/2 (incomplete phragmocone).

Geographic and stratigraphic distribution: The only specimen recorded in the Iberian Range comes from the Tenuicostatum Zone, Semicelatum Subzone of Moneva.

Measurements: see Table 1.

Description: Shell moderately evolute, WER index of 1.96; subquadrangular to slightly sub-rectangular section, with almost flat and parallel flanks. Ventral region crossed by a thick keel bordered by two thin and shallow furrows. Wide umbilical region showing rounded edges and convex walls. Ornamentation composed of small marked tubercles on the umbilical edge from which arise pairs of broad and strong ribs, approximately equal in size to the intercostal spaces, very slightly retroverse and projected forward upon reaching the ventral region. The visible part of the suture line shows LS1 smooth and divided by a relatively thick central lobe, LL1 sharp and half the size of the anterior saddle and SL2 rounded and smooth.

Remarks: The specimen identified is probably a juvenile. It differs from *B. arabicum* by the more inflated internal whorls, the strong and sparse ribs and the more numerous tubercles.

Bouleiceras ibericum nov. sp.
Figs. 6, 7
1908. *Bouleiceras nitescens* -Thévenin, pl. 2, fig. 11.
?1952. *Bouleiceras nitescens* Thévenin - Arkell, text. fig. 4.
1974. *Bouleiceras* n. sp. - Goy, p. 571, pl. 39, fig. 1a-c.
1974. *Bouleiceras* sp. - Goy, p. 571, pl. 40, figs. 1a-c.
1974. *Bouleiceras* sp. - Comas-Rengifo, p. 129, pl. 14, fig. 1a, b.
1986. *Bouleiceras* sp. - Herrero-Organero, pl. 11, fig. 5.

Derivation of the name: From the Iberian Cordillera, where it is the most frequent form of *Bouleiceras*.

Holotype: Specimen Tu10.2/1 (Fig. 6(C, D)) coming from a level located at the extreme base of the Elegantulum Subzone of the Turmiel Section. It is housed in the Paleontological collection of the

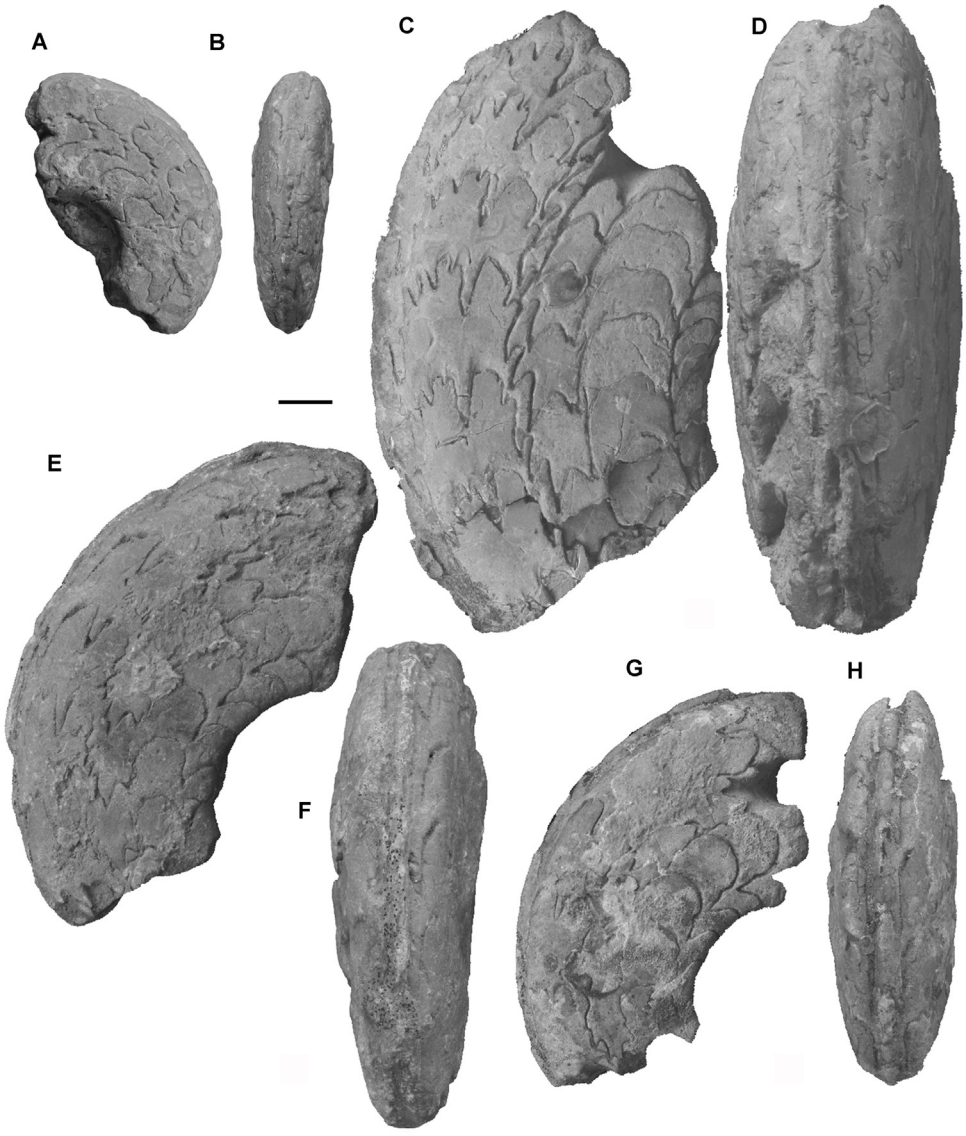

Fig. 6. *Bouleiceras ibericum* nov. sp. **A, B**. Specimen Mo5.1-2/6, Tenuicostatum Zone, Semicelatum Subzone, Moneva, in lateral (A) and ventral (B) views. **C, D**. Specimen Tu10.2/1 (holotype), Serpentinum Zone, Elegantulum Subzone, Turmiel, in lateral (C) and ventral (D) views. **E, F**. Specimen Mo5.1-2/3, Tenuicostatum Zone, Semicelatum Subzone, Moneva in lateral (E) and ventral (F) views. **G, H**. Specimen Mo5.1-2/2, Tenuicostatum Zone, Semicelatum Subzone, Moneva, in lateral (G) and ventral (H) views. Scale bar: 1 cm.

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Complutense University of Madrid (Department of Geodynamics, Stratigraphy and Paleontology).

Material: Specimens Bh-5.2/1; Tu-10.2/1; Tu-10.2/2; Ab-11/2; Mo-5.1-2/1,2,3,5,6; 1Ar-72/1 (2Ar-8/1); 1Ar-74/1 (2Ar-8/2). All of them are incomplete phragmocones.

Geographic and stratigraphic distribution: This species has been recorded in the uppermost Semicelatum Subzone of the Tenuicostatum Zone in Turmiel, Moneva and Ariño, and in the Elegantulum Subzone of the Serpentinum Zone in Barahona, Turmiel, Ablanquejo and Moneva.

Measurements: see Table 1.

Diagnosis: Shell smooth, moderately evolute. Suboval compressed section, with marked keel, bisulcate in the inner whorls. Ceratitic suture with wide saddles and deep lobes.

Description: Shell moderately evolute (WER index: 1.79 in the only adult specimen measurable); suboval compressed section with gently convex flanks, showing the maximum width near the umbilical region and converging towards the ventral region; marked and raised keel bordered by two bands slightly sunken in the first whorls, but disappearing in the later whorls. Umbilical area with rounded edge and smooth walls, vertical in inner whorls and strongly convex in later stages. The suture line presents EL1 very deep and narrow, LS1 broad, divided by a central lobe, sometimes with small acute incisions in its ventral half; LL1 narrow with semi-parallel sides, somewhat wider and with several sharp incisions on its posterior part, LS2 rounded and smooth, slightly wider than the anterior lobe, LL1 acute and of small size. Acute lobes and rounded wide chairs appear as accessory elements on the umbilical edge and walls.

Remarks: This new species is morphologically close to *B. nitescens*, differing by its sub-oval section, absence of ornamentation on internal whorls, and a more indented suture line, especially in LL2, which has more irregularly distributed incisions. As for the WER index, the only adult specimen that could be measured has a moderate value, lower than that of *B. nitescens*. The main differences with other described species of the genus are as follows: *B. elegans* is more evolute and with a more compressed section. *B. arabicum* is also more evolute and with a more compressed section, showing a more indented LS1. *B. tumidum* is more involute, with a more globose (even sub-trapezoidal) section. *B. marraticum* have a different, subquadrangular section, and prominent ornamentation.? *B. betetensis* nov. sp. is also more involute, with a more compressed and sharpened section and a less indented suture line.

?*Bouleiceras betetensis* nov. sp.

Fig. 8

Derivation of the name: Referred to the locality of Valsalobre de Beteta (Cuenca).

Holotype: Specimen Va-5.2/3 (Fig. 8(D, E)) coming from the Serpentinum Zone, Elegantulum Subzone, of Valsalobre de Beteta. It is housed in the Paleontological collection of the Complutense University of Madrid (Department of Geodynamics, Stratigraphy and Paleontology).

Material: Two incomplete phragmocones: 1Eb-5.2/1 (paratype; Fig. 8(A-C)) and Va-5.2/3.

Geographic and stratigraphic distribution: This species has been recorded only in the Serpentinum Zone, Elegantulum Subzone, of Entrambasaguas and Valsalobre de Beteta.

Diagnosis: Shell smooth, involute. Subtriangular section, strongly compressed. Elevated keel. Ceratitic suture.

Description: Shell moderately involute. Subtriangular compressed section, the last visible whorl covering half of the previous one. No ornamentation is observed. The ventral region is rounded, with a thin and elevated keel. The umbilicus presents marked edges, somewhat rounded, and flat and very vertical walls. EL1 deep and acutely sharpened; ES1 wide, without incisions and divided by a narrow and acute central lobe that reaches a depth of almost the middle of the saddle; LL1 narrower than the previous saddle, with several sharp incisions in the posterior part and the sides smooth and semi-parallel, LS2 larger than the anterior lobe, rounded, deep and smooth. The following lobes are small but sharp and the saddles wide and rounded until reaching the umbilical wall.

Remarks: The suture line of this species is consistent with that of *Bouleiceras*, although both saddles and lobes are slightly less indented. However, the specimens studied show no ornamentation, their umbilicus is smaller, and the sections are clearly subtriangular. This combination of characteristics makes it possible to differentiate this species from any other species of this genus (Fig. 9), being more similar to what is observed in species of *Nejdia* Arkell, 1952 such as *N.*

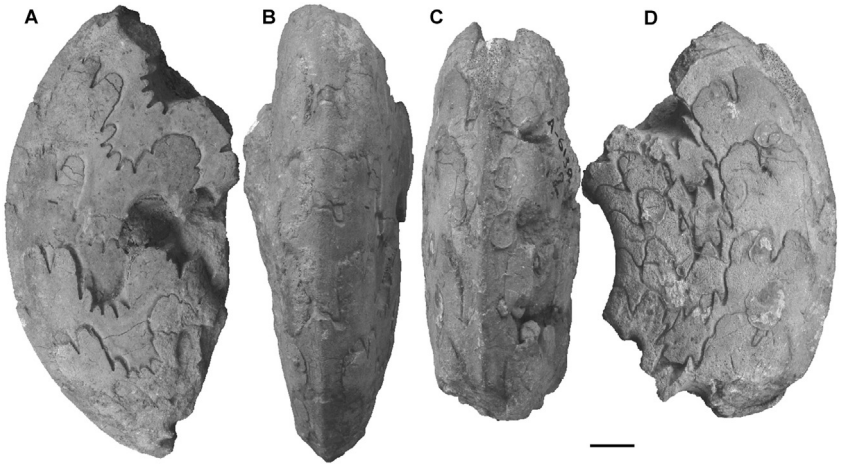

Fig. 7. *Bouleiceras ibericum* nov. sp. **A, B**. Specimen Ar74/1, Tenuicostatum Zone, Semicelatum Subzone, Ariño, in lateral (A) and ventral (B) views. **C, D**. Specimen Ab11/2, Serpentinum Zone, Elegantulum Subzone, Ablanquejo, in ventral (C) and lateral (D) views. Scale bar: 1 cm.

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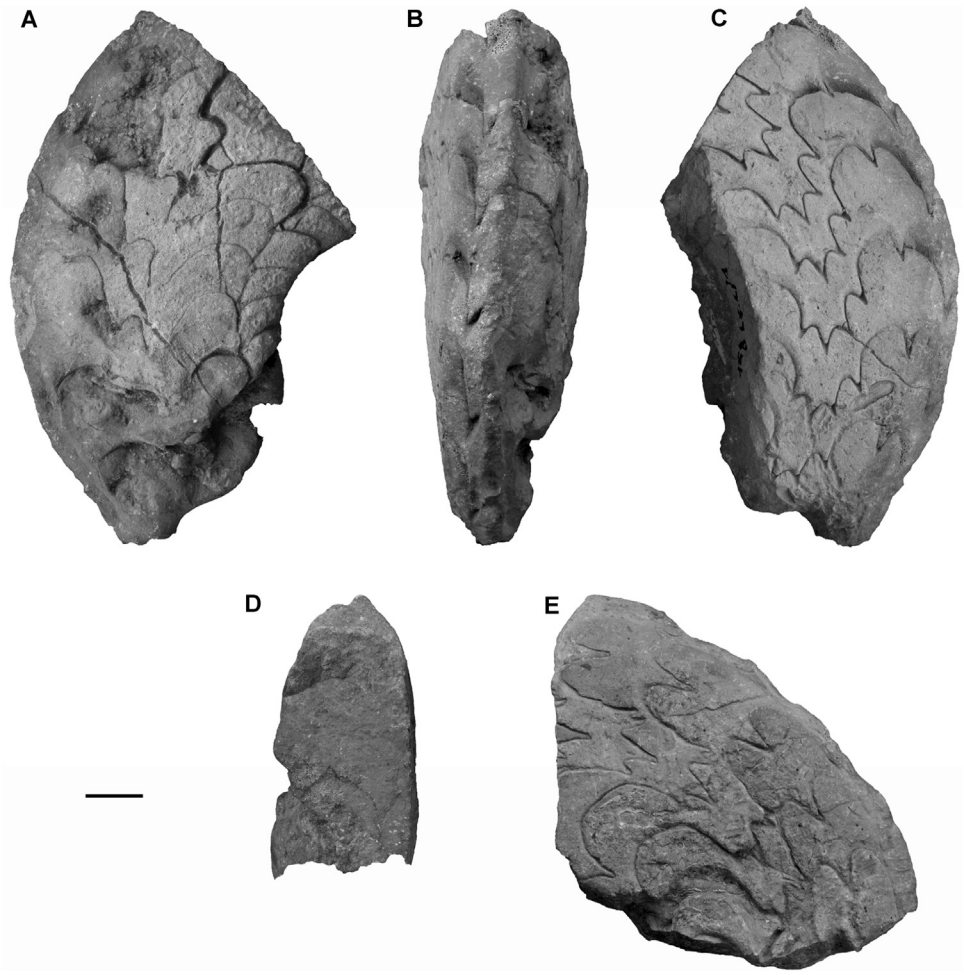

Fig. 8. *Bouleiceras? betetensis* nov. sp., Serpentinum Zone, Elegantulum Subzone, Valsalobre de Beteta. **A-C**. Specimen 1Eb-5.2/1 (paratype) in lateral (A), ventral (B) and lateral-opposite (C) views. **D, E**. Specimen Va-5.2/3 (holotype) in ventral (D) and lateral (E) views. Scale bar: 1 cm.

bramkampi Arkell, 1952 or *N. pseudogruneri* (Thévenin, 1908). For this reason, the generic determination of? *B. betetensis* nov. sp. is uncertain and a question mark has been placed related to the generic name. It is worth remembering that, according to Guex (1974), *Nejdia* appears to be phylogenetically related to *Bouleiceras*, and both *N. bramkampi* and *N. pseudogruneri* have been recorded in the Serpentinum Zone of the Iberian Range (Goy and Martínez, 1996).

Discussion

Stratigraphic distribution of the Bouleiceras *species*

In the Iberian Basin, the oldest species of *Bouleiceras* is *B. elegans*, recorded from the middle part of the Semicelatum Subzone (Herrero Matesanz, 1995), possibly from the Tenuicostatum biohorizon. Immediately above, in the Semicelatum Subzone, Semicelatum biohorizon, *B. arabicum* and *B. marraticum* have been found. None of these three species appear above the upper boundary of the Tenuicostatum Zone (Figs. 2,3). In the Semicelatum biohorizon also appears *B. nitescens*, a possibly older species which shows some similarities with *B. chakdallaense* and persists in the Elegantulum Subzone of the Serpentinum Zone. The specimen of *B. nitescens* figured by Bizon et al. (1966) from the Levantine Sector of the Iberian Range is associated with several brachiopod species that only coexist at levels of the Semicelatum Subzone of the Tenuicostatum Zone (García Joral and Goy, 2000; Baeza-Carratalá et al., 2016). Other species, like *B. ibericum* nov. sp. and *B. tumidum* have also been recorded in the upper part of the Tenuicostatum Zone and in the lower part of the Serpentinum Zone. *B.? betetensis* nov. sp. has been recorded only in the Elegantulum Subzone (Figs. 2,3).

Outside the Iberian Range, the oldest *Bouleiceras* species should be *B. chakdallaense*, recorded in the middle member of the Datta Formation (probably in the Tenuicostatum Zone) of Northeastern Pakistan, showing remarkable affinities with *B. elegans* from Madagascar, Arabia and Spain. *Bouleiceras* cf. *chakdallaense* has been identified in Chile by Hillebrandt and Schmidt-Effing (1981) at levels corresponding to the Tenuicostatum Zone, Simplex Subzone, which is roughly equivalent in the Sub-Mediterranean Province to the Tenuicostatum Zone, Paltum Subzone, and the lower part of the Semicelatum Subzone (Page, 2003). In the same member of the Datta Fm. of Northeastern Pakistan is also recorded *B. nitescens*, a species also bituberculated in the internal whorls. The first record of this species in Madagascar and Arabia is imprecise but it is probably located in the Semicelatum Subzone of the Tenuicostatum Zone. In Portugal, the specimens figured by Mouterde (1953) as *Bouleiceras* cf. *nitescens* and *Bouleiceras* sp. from Ribeiro da Povoa (South of Coimbra) and by Mouterde and Rocha (1981) as *Bouleiceras nitescens*? from the Couros river area (North of Tomar), are associated to *Hildaites* and attributed to the lower part of the Levisoni Zone (equal to Serpentinum Zone of the NW European province). However, in the case of the Ribeiro da Póvoa specimens, it cannot be discarded that they come from the

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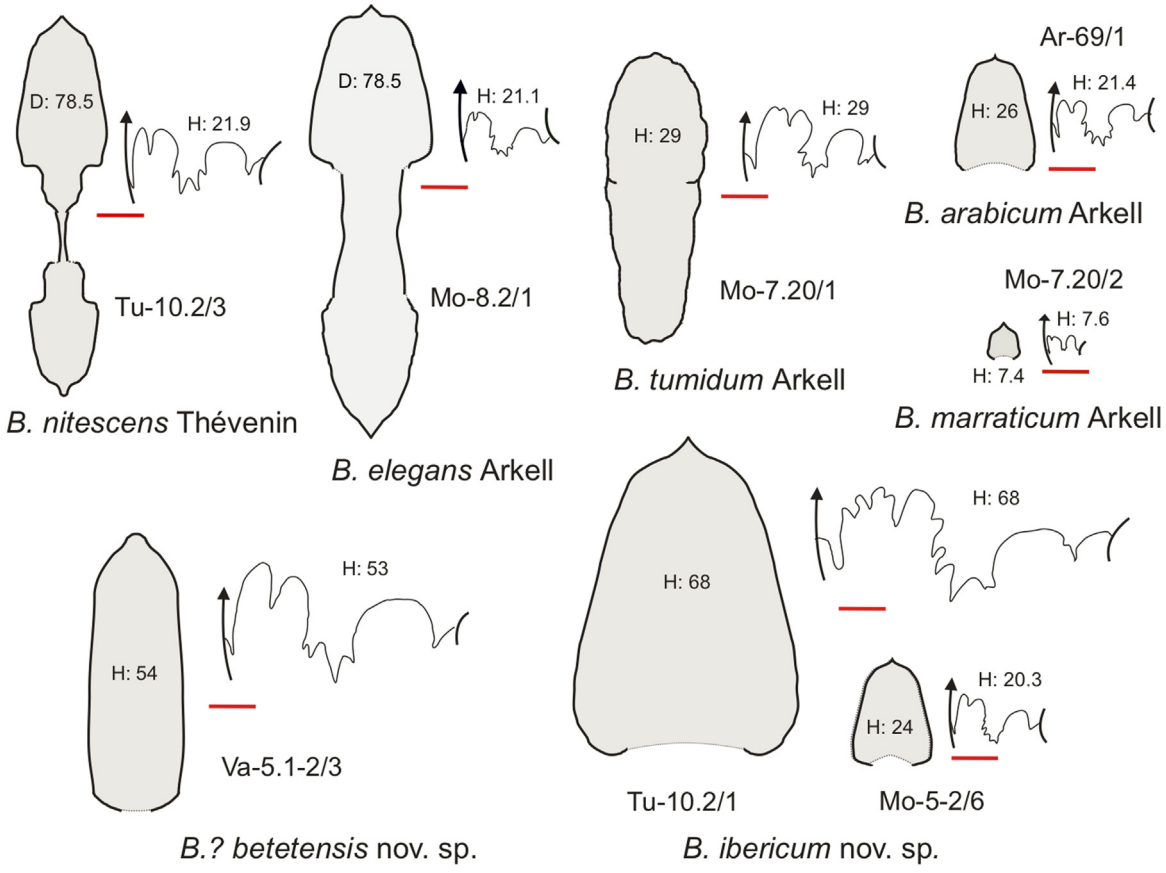

Fig. 9. Sections and suture lines of the *Bouleiceras* species studied. Scale bars: 1 cm.

uppermost part of the Polymorphum Zone (equivalent to the Tenuicostatum Zone of the NW European province) since they are also associated with *Protogrammoceras madagascariense* and the brachiopod *Calyptoria vulgata* (Cooper, 1989), which rarely exceed the boundary between the Polymorphum and Levisoni Zones.

Among the other species described by Arkell (1952) in Arabia, *B. arabicum* has been recorded also in Kenya (Ayer, 1952; Arkell, 1952) and the Iberian Range; *B. marraticum* is only known in its type locality and in the Iberian Range, where it does not reach the boundary between the Tenuicostatum and Serpentinum zones; and *B. rectum* has been cited from Madagascar, Arabia (Arkell, 1952) and Somalia (Chiocchini et al., 2002), supposedly in the Serpentinum Zone, although its association with "*Spiriferina madagascariensis*" (= *Calyptoria* sp.) in Somalia probably means that it may be present in the uppermost Tenuicostatum Zone. Other species such as *B. tumidum* and *B. ibericum* nov. sp. (Madagascar and Iberian Range) are recorded in the upper part of the Tenuicostatum/Polymorphum Zone and in the lower part of the Serpentinum/Levisoni Zone. Faugères (1975) cited *Bouleiceras* aff. *arabicum* Arkell from Jbel Dehar in N'Sour (Morocco) from 60 m below the lower boundary of the Bifrons Zone, as well as "*Bouleiceras* associated to *Hildaites* or to *Harpoceratoides* and *Hildaites*", assigned to the Serpentinum Zone. In Chile, apart from *B.* cf. *chakdallaense*, another species *Bouleiceras chilense* Hillebrandt, 1973 has been described from the Hoelderi Zone, equivalent to the Falciferum/Serpentinum Zone of Western Tethys (Hillebrandt and Schmidt-Effing, 1981). This species shows a remarkable similarity with *B. elegans* for its similar ontogenetic development. Finally,? *B. betetensis* nov. sp., with umbilicus and section very close to those of *Nejdia* and suture line as in *Bouleiceras*, is among the species with a later record in the Elegantulum Subzone. It is only known from the Iberian Range and its stratigraphic position is almost equal to the one shown by *B. chilense* in the Andean region.

The record of *Bouleiceras* seems to be limited to the Tenuicostatum/Polymorphum Zone and the lower part of the Serpentinum/Levisoni Zone. The genus first occurred in the lower part of the Tenuicostatum Zone in Chile and probably Pakistan, and from the Semicelatum Subzone upwards in Arabia, Northeastern and Northwestern Africa, and the Iberian Peninsula. Apparently, no species has been found above the Elegantulum Subzone. The stratigraphical distributions of all *Bouleiceras* species described in this paper are shown in Fig. 10, either directly from the published data or inferred as previously discussed.

Evolution and dispersal of Bouleiceras

According to Guex (1974), the origin of the genus *Bouleiceras* should be sought in the Hildoceratacеae of the latest Pliensbachian showing periumbilical tubercles, as in *Canavaria* Gemmellaro, 1886 and *Tauromeniceras* Mouterde, 1967, which group evolute, tuberculated, and ribbed forms with simple suture line. This origin is supported by cladistic analysis (Rulleau et al., 2003Bardin et al., 2017). Most likely, it probably derives from some species of *Tauromeniceras* from the terminal part of the Spinatum Zone, Hawskerense Subzone (equivalent to the Emaciatum Zone, Elisa Subzone in the Mediterranean Province), close to *T. elisa* (Fucini) or *T. nerina* (Fucini). Both species show a ventral region provided with a keel flanked by two depressed areas that become into furrows as the growth of the shell progresses. Its ornamentation consists of straight, slightly retroverse ribs, with small tubercles at the umbilical end and – at the last whorl – also thickenings or tubercles near the umbilical edge (Braga, 1983: pp. 308-313, pl. 15, 4-10).

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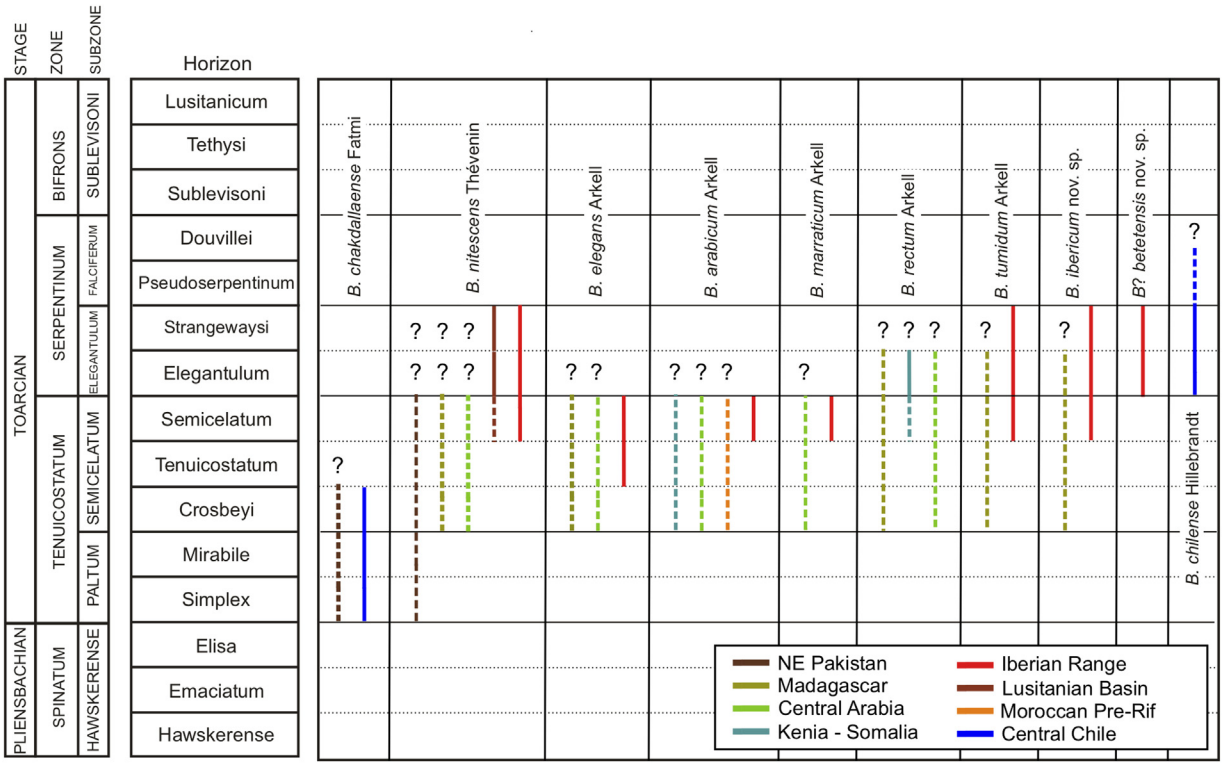

Fig. 10. Chronostratigraphic distribution of the *Bouleiceras* species in the different basins where this genus is recorded. Solid line: observed distribution; dashed line: inferred distribution. See the text for more explanations.

These species have been recorded in Southern Europe, including Betics, Iberian Basin, Lusitanian Basin, Sicily and the Apennines (Fucini, 1931; Ferretti, 1967; Mouterde, 1967; Comas Rengifo, 1982; Braga, 1983). The *Tauromeniceras-Bouleiceras* transition would involve the attenuation of the ornamentation in the external whorls and an increase of involution. The geographical area where this transition took place is not properly known. In the Semicelatum Subbiochron, the paleogeographical distribution and diversity of the genus reach its maximum, being its last records from the early Serpentinum Zone.

Rulleau et al. (2003) point out that the Andean forms of *Bouleiceras* are small, slightly more precocious, with little relation whit almost all of Malagasy types, and could represent vicariant evolution. Riccardi (1991) on the basis of ammonoids distributions considered that marine connection between Eastern Tethys and South America was in the Lower Jurassic through the Australian margin of Gondwana and, from the Pliensbachian onward, connection with Western Tethys occurred through the sporadically opened "Hispanic Corridor" in Central America. In this sense, the most recent presumed age of *B. chilense* suggests that it could derive from populations of *B. elegans* reaching the Andean Area from the Western Tethys through the Hispanic Corridor (Fig. 11). However, the arrival of primitive forms of the genus from Western Tethys to South America via the Hispanic Corridor in the early Tenuicostatum Zone is more speculative, since these primitive forms (as *B. chakdallaense*) have not been recorded in the Western Tethys. On the other hand, *Canavaria* and *Tauromeniceras* are present in the Andean region (Hillebrandt, 2006; Riccardi, 2008).

Ammonoid taxa show often a very wide or cosmopolitan distribution, that implies a high dispersal ability, but the latitudinally restricted distribution of *Bouleiceras*, between 30 °N and 30 °S (Fig. 11) seems to be controlled by temperature constraints. Martínez (2017b) postulated that other genera of the same subfamily (*Paroniceras*, *Frechiella* and *Oxyparoniceras*) have been influenced in their geographical distribution more by latitudinal constraints (temperature) than by bathymetry or other factors. Furthermore, the distribution of *Bouleiceras* shows a notable parallelism with that of the contemporaneous brachiopod *Calyptoria* (Cooper 1989), that has been interpreted by Baeza-Carratalá et al. (2018) as controlled mainly by temperature. Paleotemperature increased globally in the late Tenuicostatum and the Eaely Serpentinum zones by 7 °C (Bailey et al., 2003; McElwain et al., 2005; Gómez et al., 2008; Gómez and Goy, 2011, Ruebsam et al., 2019), reaching in wide areas values similar to the equatorial conditions of the Arabian region. This warming is associated with high sea levels (Hallam, 1997; Ruesbam et al., 2019) probably favoring the circulation of big masses of water from the Western Tethys to the Panthalassa trough the Hispanic Corridor. That could have triggered a sort of "suction effect" that would accelerate the westward current in the South of Tethys and the southward current through the Viking Corridor, enhanced at this time as shown by Arias (2007). The effects of this change in currents must have been very strong, not only enabling the dispersal of faunas to the west but also favoring the disruption of provincialism observed in many groups (García Joral and Goy, 2000; Damborenea, 2002; Macchioni and Cecca, 2002; Rulleau et al., 2003; Arias, 2006b; Dera et al., 2010; Andrade et al., 2016).

If the distribution of *Bouleiceras* was conditioned by water temperature, the Australian Way does not seem very suitable, since currents to the east in medium latitudes would probably be too cold and slow for this purpose, precluding dispersal from the Indo-Madagascan area to South America through Australia (Arias, 2008). New findings of *Bouleiceras* in the Northern Gondwana paleomargin or other regions will surely be needed to help resolve the issue of the origin and dispersal of this genus.

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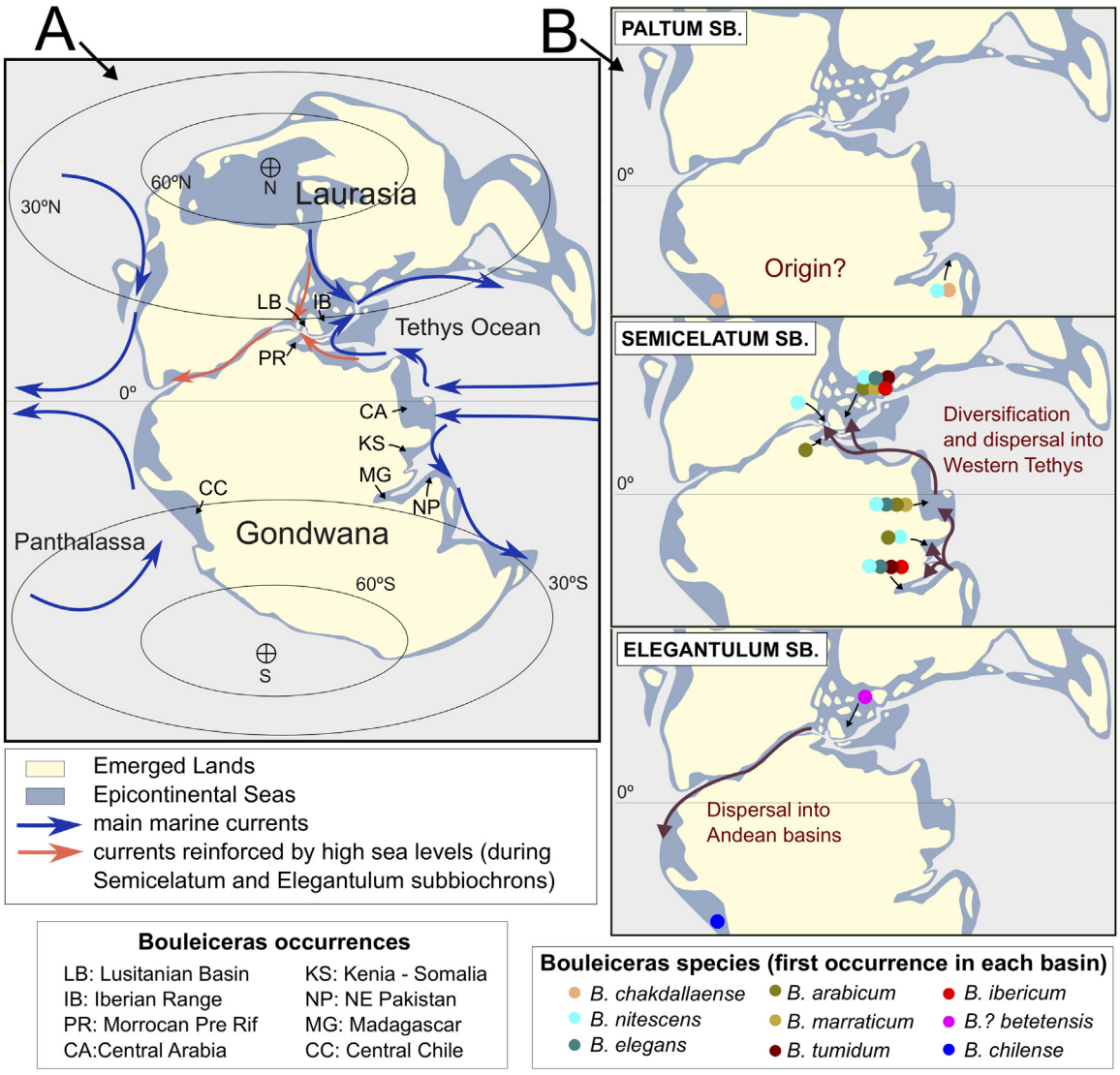

Fig. 11. A. Paleogeographic map of the world in the early Toarcian, showing the position of the basins where *Bouleiceras* has been recorded (modified after Damborenea, 2002 and Baeza-Carratalá et al., 2018). The main ocean currents assumed for this time are indicated (after Arias, 2006a, 2008). **B**. Paleogeographic maps for the Paltum, Semicelatum and Elegantulum subzones showing the first occurrences of the species of *Bouleiceras* in each basin and the hypothetical routes of dispersal of the genus.

Conclusions

The systematic revision of the specimens attributed to *Bouleiceras* from the Iberian Range has led to the recognition of seven species of this genus, including two new taxa: *B. nitescens* Thévenin, *B. elegans* Arkel, *B. arabicum* Arkel, *B. marraticum* Arkel, *B. tumidum* Arkel, *B. ibericum* nov. sp., and *B.? betetensis* nov. sp. All these species come from the Central and Levantine sectors of the basin and have been recorded in the Semicelatum Subzone of the Tenuicostatum Zone and in the Elegantulum Subzone of the Serpentinum Zone. These data, together with the known record of the genus in other regions, make it possible to establish more accurately the stratigraphic distribution of *Bouleiceras* in the Tenuicostatum Zone and the lower part of the Serpentinum Zone. The genus *Bouleiceras* probably derives from some species of *Tauromeniceras* from the Hawskerense Subzone of the Spinatum Zone. From these primitive forms (as *B. chakdallaense*) would have arisen most of the species of this genus (*B. nitescens*, *B. elegans*, *B. arabicum*, *B. marraticum*, *B. tumidum*, *B. ibericum* nov. sp.) which dispersed through the northern margin of Gondwana to the Westernmost Tethys. The most recent presumed age of *B. chilense* suggests that it could have derived from populations of *B. elegans*. Finally, *B.? betetensis* nov. sp. seems to be a transitional species to the genus *Nejdia*, that is recorded in the Falciferum Subzone of the Serpentinum Zone of the Iberian Range. The area of origin and the dispersal routes of *Bouleiceras* remain unclear, but their distribution seems to follow high temperature conditions and would have been favored by high sea levels.

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